

Does food availability affect energy expenditure rates of nesting seabirds? A supplemental-feeding experiment with Black-legged Kittiwakes (*Rissa tridactyla*)

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Abstract: We used a supplemental-feeding experiment, the doubly labeled water technique, and a model-selection approach based upon the Akaike Information Criterion to examine effects of food availability on energy expenditure rates of Black-legged Kittiwakes (*Rissa tridactyla*) raising young. Energy expenditure rates of supplementally fed females ($n = 14$) and males ($n = 16$) were 34 and 20% lower than those of control females ($n = 14$) and males ($n = 18$), respectively. Energy expenditure rates of females were more responsive to fluctuations in food availability than those of males. Fed males likely expended more energy while off the nest than fed females, possibly because of nest defense. Energy expenditure rates of fed kittiwakes were similar to values reported for kittiwakes that were either not raising young or not foraging. Parent kittiwakes, therefore, adjusted parental effort in response to variation in breeding conditions due to changes in food availability. Adjustments in reproductive effort in response to variable foraging conditions may have significant effects on the survival and productivity of individuals, and thus provide substantial fitness benefits for long-lived seabirds such as Black-legged Kittiwakes.

Résumé : Nous avons utilisé une expérience d'addition de nourriture, la technique de l'eau doublement marquée et un modèle de sélection basé sur le critère d'information d'Akaike pour étudier les effets de la disponibilité de la nourriture sur les taux de dépense énergétique chez des mouettes tridactyles (*Rissa tridactyla*) pendant l'élevage des jeunes. Les taux de dépense énergétique des femelles ($n = 14$) et des mâles ($n = 16$) qui ont reçu des suppléments de nourriture sont respectivement de 34 % et de 20 % moins élevés que ceux de femelles ($n = 14$) et de mâles ($n = 18$) témoins. Les taux de dépense énergétique des femelles sont plus sensibles aux fluctuations de la disponibilité de la nourriture que ceux des mâles. Les mâles nourris dépensent probablement plus d'énergie hors du nid que les femelles nourries, peut-être parce qu'ils assurent la défense du nid. Les taux de dépense énergétique des mouettes nourries sont semblables aux valeurs rapportées dans la littérature dans le cas de mouettes qui n'élèvent pas de jeunes ou qui ne font pas de quête de nourriture. Les mouettes ajustent donc leur effort parental en fonction des variations des conditions de la reproduction, elles-mêmes dépendantes de la disponibilité de la nourriture. L'ajustement de l'effort reproducteur aux conditions variables de quête de nourriture peut avoir un effet significatif sur la survie et la productivité individuelles, ce qui a pour conséquence d'améliorer le fitness de façon importante chez les oiseaux marins, tels que la mouette tridactyle.

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Introduction

The energetic costs associated with reproduction in general and provisioning of young in particular are the highest an adult bird will experience throughout its lifetime, except

perhaps during migration (Bryant 1997). The high energetic costs that parents incur while provisioning young are due largely to increases in foraging time, which often involve very costly flight behaviors such as plunge-diving in seabirds (Adams et al. 1991) or short, dynamic flights in pas-

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serines (Bautista et al. 1998; Nudds and Bryant 2000). The benefit of this increase in parental energy expenditure is that it tends to lead to an increase in provisioning rate, which in turn positively affects chick growth rate and productivity (Bryant 1991; Visser 2001). This is why parental energy expenditure is considered to be a good measure of parental effort (Trivers 1972; Deerenberg et al. 1995; Potti et al. 1999). Parents can also incur, however, a survival cost from increased energy expenditure during brood rearing. For example, Deerenberg et al. (1995) and Golet et al. (2000) both demonstrated that increased parental energy expenditure rates associated with brood rearing led to decreased survival in avian parents. A similar trend has been observed in other taxa as well (Schmid-Hempel and Wolf 1988). Therefore, a trade-off between reproductive investment and adult survival may exist. Parents, especially those that are relatively long-lived, should reduce parental effort (i.e., energy expenditure) under conditions in which the probability of rearing young is so low as to maximize parental survival and lifetime reproductive success (Williams 1966; Stearns 1992). This suggests that factors which regulate parental effort may also define reproductive strategies.

Food availability is one factor that may regulate parental effort (Norberg 1977; Bryant and Westerterp 1983; Lalonde 1991; Davis et al. 1999). Empirical evidence suggests, however, that the direction and strength of the relationship between food availability and parental energy expenditure may differ within and between species (Bryant and Tatner 1988, 1991). Foraging mode, spatiotemporal variability in the food supply, or the cost of reproduction to the adult and hence the level of parental investment favored by natural selection have all been suggested as primary factors affecting this relationship (Tinbergen and Dietz 1994; Wiehn and Korpimäki 1997). Opportunities to investigate the relationship between parental energy expenditure and food availability in both sexes in a controlled setting have been rare, however, so it remains unclear which factors have the most influence on the direction and strength of the relationship.

Our goal was to assess the relationship between food availability and energy expenditure of parent seabirds raising nidicolous young. We conducted this experiment on free-ranging Black-legged Kittiwakes (*Rissa tridactyla*) at a colony in the northern Gulf of Alaska. Our objectives were (i) to determine if the energy expenditure rates of parent kittiwakes provided with supplemental food (hereinafter fed birds) differed from those of control parents, and (ii) to determine the strength of the relationship between parental energy expenditure rates and a suite of extrinsic (i.e., food availability, brood size, nestling age) and intrinsic (i.e., body size, body condition, and gender of adults) covariates and factors. We predicted that energy expenditure rates would be lower in fed parents because the food supplement was sufficient to provide for all the energy needs of the nestlings and parents. The need for parents to forage at sea should therefore be reduced and hence parental energy expenditure should also be reduced. Furthermore, parental energy expenditure rates have been shown to be positively related to chick-rearing activities in this species, while adult survival has been shown to be negatively associated with chick-rearing activities (Jacobsen et al. 1995; Golet et al. 1998, 2000). Therefore,

fed parents offered an opportunity to decrease energy expenditure rates without adversely affecting the current year's productivity should do so in order to increase their probability of survival.

Materials and methods

Black-legged Kittiwakes are small gulls (Laridae) that nest colonially on sea cliffs throughout much of the circumpolar north. Kittiwakes are monogamous, exhibit biparental care during incubation and brood rearing, and in Alaska, tend to lay one- or two-egg clutches. Major prey in this part of the species' range, captured predominantly via plunge-diving, include pelagic schooling fishes such as Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), lanternfishes (Myctophidae), and, to a lesser extent, planktonic Crustacea such as euphausiids (e.g., *Thysanoessa* spp.). The sexes are the same color but males are slightly larger than females (Jodice et al. 2000).

We conducted the experiment on Middleton Island, Alaska, which is located in the northern Gulf of Alaska approximately 80 km south of Prince William Sound. The kittiwakes used in this study nested on an abandoned radar tower, which was enhanced by placing 212 nest-sized ledges along its outer walls (for details see Gill and Hatch 2002). Each ledge was equipped with a 30 cm high by 26 cm wide opening that was fitted with a sliding glass window (one-way visibility) accessible to us from inside the tower. We provided 235 g of thawed capelin 3 times daily (early morning, midday, and late afternoon) to 38% of active nest ledges during chick rearing via a tube immediately adjacent to the nest ledge (fed treatment; Gill and Hatch 2002; Gill et al. 2002). This represents about 1.75 times adult body mass and was sufficient to meet all the energy needs of the nestlings and parents. Both adults and chicks consumed the supplemental food. Remaining nest ledges were not provided with supplemental food (control treatment).

We measured energy expenditure rates of fed and control parents between 27 and 31 July 1998 with doubly labeled water (DLW; Lifson and McClintock 1966). Kittiwake chicks generally fledge at 37–45 days post hatch on Middleton Island (Gill et al. 2002) and, at the time of our experiment, the mean age of nestlings was 26.7 ± 4.3 (± 1 SD) days post hatch (range = 18–36 days). We restricted the experiment to adults with chicks in this general age range to minimize potential differences in adult provisioning effort, and hence energy expenditure rate, owing to the low food-intake capacity of younger nestlings (Gabrielsen et al. 1992).

We captured all fed kittiwakes and most control birds at the tower on their nests via the sliding windows ($n = 75$). Five additional control birds were captured on nests at an abandoned building 300 m from the tower. Average adult energy expenditure, adult body mass, adult body size, brood size, and age of the oldest chick in the nest for these five control birds were nearly identical with those of control birds captured on the tower.

We measured length of head plus bill (hereinafter head-bill, ± 0.1 mm), flattened-wing length (± 0.1 mm), tarsus length (± 0.1 mm), and body mass (± 0.1 g using an Ohaus triple-beam balance) for each bird. We recorded the number of

chicks in the brood and aged them on the basis of either known hatch dates ($n = 37$ nests on the tower) or regression models of wing length on age based on known-age chicks ($n = 5$ nests off the tower; Gill et al. 2002). All birds captured at the tower had been banded previously and sex was determined from genetic analyses of blood; birds captured away from the tower were sexed using morphometrics (Jodice et al. 2000).

Birds were given an intraperitoneal injection of 0.4 mL of a mixture of DLW (59.0% ^{18}O , 34.4% ^2H) immediately after capture. This dosage allowed for collection of blood samples up to 30 h post equilibration, with ^{18}O levels sufficiently elevated above background to allow for accurate measurement of CO_2 production. Immediately following injection, birds were wrapped in cloth bags and placed in a dark box for 1 h to permit equilibration. We then collected an initial 100- μL blood sample from the brachial vein, flame-sealed the sample in a series of non-heparinized microhematocrit tubes, and kept the samples refrigerated at ca. 5°C until they were analyzed. We released injected birds outside the tower immediately following collection of the blood sample. We monitored nests of injected birds to assess behavior and nest attendance post release. We recaptured injected kittiwakes on their nests 23–30 h following release, then weighed them and collected a final blood sample using methods described above. We established background isotope levels by capturing and collecting blood samples from six kittiwakes at the tower that had not been injected.

G.H.V. measured isotope concentrations in water distilled from all collected blood samples using the CO_2 equilibration technique. Isotope analyses were run in triplicate to assure accuracy of CO_2 production estimates. We used eq. 7.17 from Speakman (1997) when calculating rates of CO_2 production to account for fractionation effects, assuming that 25% of the water efflux is lost through evaporative pathways (Visser 2001). Fractional ^2H and ^{18}O turnover rates were calculated using the population-specific background concentrations for these isotopes, and the individual-specific isotope concentrations of the initial and final blood samples.

We expressed CO_2 production rates on a mass-specific basis ($\text{mL CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$; hereinafter referred to as mass-specific field metabolic rates (msFMR)) because this removes body mass as a source of variation in individual energy expenditure rates. We also present field metabolic rates (FMRs) as daily energy expenditure (kJ/d per bird), which was calculated on the basis of equations in Speakman (1997) and using an energetic equivalent of 27.33 kJ/L CO_2 respired, which is appropriate for a protein- and lipid-rich diet (Gessaman and Nagy 1988).

We examined the relationship between msFMR and measurement interval (i.e., the time elapsed between initial and final blood sample collection, which ranged from 22.9 to 30.4 h) to determine if measurement of energy expenditure might be biased by any diurnal pattern in kittiwake activity (Speakman 1997). We found no relationship between the deviation of the measurement interval from 24 h (dev24) and the msFMR of fed birds ($\text{msFMR}_{\text{fed}} = 2.16 - 0.03 \times \text{dev24}$; $t_{29} = 0.51$ for the slope term, $P = 0.6$), therefore we used unadjusted msFMR values in subsequent analyses for fed birds. There was, however, a significant positive relationship between

the msFMR of control birds and dev24 ($\text{msFMR}_{\text{control}} = 2.95 + 0.30 \times \text{dev24}$; $t_{30} = 4.39$ for the slope term, $P < 0.001$). We corrected control msFMR values by adding the intercept term from the regression model for control birds (i.e., 2.952, or msFMR when dev24 = 0) to the difference between the observed and predicted msFMR for each individual (i.e., the residual) from the above regression model (Speakman 1997). These corrected values were used in all subsequent analyses for control birds.

Water-flux rates of injected kittiwakes were calculated on the basis of equations in Nagy and Costa (1980), modified for fractionation effects by Visser et al. (2000b, eq. 6, assuming that 25% of water flux is lost through evaporative pathways). The total amount of body water was determined on the basis of the principle of ^{18}O dilution, using the population-specific background value, the quantity of the dose, the ^{18}O -enrichment of the dose, and the ^{18}O enrichment after equilibration (Visser et al. 2000a, eq. 2, following the "plateau method"). The total amount of body water, in grams, was then converted to percent total body water (percentage of initial body mass) for each individual.

Statistical analyses

We used a suite of analysis of covariance (ANCOVA) models along with a model-selection approach based on the Akaike Information Criterion (AIC; Burnham and Anderson 1998) to quantify the effects of food availability and numerous covariates on parental energy expenditure. The advantages of the model-selection approach over analyses based on a single model or a stepwise process are that the former allows information from more than one model to be used, results in more precise parameter and variance estimates for each variable, ranks models in order of the probability of each model being the best, given the available data, and, because it evaluates multiple models, allows for the simultaneous assessment of multiple hypotheses (Burnham and Anderson 1998).

We conducted nine ANCOVAs each for females and for males (Table 1). Each model included a subset of independent variables selected from the following list: feeding treatment (fed or control; categorical), brood size, adult body mass at capture (adjusted for treatment), body size (sum of standardized head-bill, flattened-wing, and tarsus lengths, each of which weighted the first principal component from a factor analysis evenly; Jodice et al. 2000), and chick age (age, in days post hatch, of the older of two chicks in a two-chick brood or the singleton in a one-chick brood). We did not combine continuous variables that were strongly correlated or factors and covariates that were strongly related within the same ANCOVA model (Neter et al. 1990). For this reason we conducted the primary analyses separately for each sex (i.e., we found that sex was strongly related to many of the other explanatory variables) and we did not include percent total body water (index of body fat reserves) as an explanatory variable because it was so strongly associated with feeding treatment.

Each ANCOVA model (Table 1) was constructed to represent a specific hypothesis regarding the effects of independent variables on parental energy expenditure. For example, model 1 for both females and males assesses the probability

Table 1. Parameters used in sex-specific ANCOVA models for analysis of mass-specific field metabolic rates ($\text{mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) of chick-rearing Black-legged Kittiwakes (*Rissa tridactyla*) in a supplemental-feeding experiment on Middleton Island, Alaska, 27–31 July 1998.

Model No.	Parameters
1	Feeding treatment, body size, body mass ^a , chick age, brood size, feeding treatment \times body size, feeding treatment \times body mass, feeding treatment \times brood size, feeding treatment \times chick age
2	Feeding treatment, body size, body mass, chick age, brood size
3	Feeding treatment, body size, body mass, feeding treatment \times body size, feeding treatment \times body mass
4	Feeding treatment, body size, body mass
5	Body size, body mass
6	Feeding treatment, brood size, chick age, feeding treatment \times brood size, feeding treatment \times chick age
7	Feeding treatment, brood size, chick age
8	Brood size, chick age
9	Feeding treatment

^aStandardized for treatment.

of energy expenditure being affected by many independent intrinsic and extrinsic factors (e.g., body size, treatment, brood size) as well as their interactions. Other models were less complex, with some representing brood effects (e.g., model 8), individual-based effects (e.g., model 5), treatment effect (model 9, which tested our primary hypothesis of energy expenditure varying by treatment alone), or some combination of these.

We ran each ANCOVA from Table 1, then followed four steps. First, we calculated the AIC statistic (corrected for sample size, AIC_c) for each model (Burnham and Anderson 1998, pp. 48–51). Second, we ranked the models according to their corrected AIC values. The model with the lowest AIC_c value was considered the most parsimonious and plausible for the available data and the models tested. We calculated the difference in AIC_c values between the highest ranked, or most parsimonious, model and each other model under consideration (i.e., ΔAIC_c) and also calculated the AIC_c weight that provides a measure of the probability that the model in question is the best model tested, given the data (eq. 4.2 in Burnham and Anderson 1998). Third, we composed a 95% confidence set of models, which is the set of models that would include the actual best model in 95% of all samples. This set includes all models where the cumulative sum of the AIC_c weights of each model, when considered in order from lowest to highest AIC_c value, sum to approximately 0.95.

Finally, to quantify the effects of each independent variable on msFMR, we calculated unconditional estimates of coefficients and standard error (SE) terms for each independent variable using eqs. 4.5 and 4.11, respectively (Burnham and Anderson 1998). Model-averaged parameter and SE estimates were then interpreted identically with any coefficient estimate from any regression analysis, i.e., the value of the coefficient and its SE estimate the slope of (for continuous terms) or difference in (for categorical terms) msFMR in relation to the independent variable being considered. Furthermore, the ratio of the coefficient estimate to the SE estimate assesses the uncertainty associated with the coefficient estimate. Variables or interaction terms not included in any of the models comprising the 95% set were regarded as unimportant and thus parameter estimates were not calculated for them (Burnham and Anderson 1998). Those variables appearing in only one model from the 95% confidence set were not suited to

parameter estimation via model averaging; for these we simply used the single coefficient and SE estimates from the appropriate model.

Means are reported as ± 1 SD and regression coefficients as ± 1 SE unless stated otherwise.

Results

We injected 80 parent Black-legged Kittiwakes with DLW and recaptured 63 (78.7%). This sample included both members of 13 pairs of fed birds and 9 pairs of control birds. We detected no evidence of compensation in parental effort between mated individuals after accounting for the overlap in the mated-pairs measurement intervals (partial correlation, $r = +0.4$, $P > 0.05$, $n = 22$). Consequently, we regarded msFMR measurements from members of a mated pair as independent.

All injected birds returned to their nest to attend chicks after the first and second captures, and all of the chicks from nests with injected parents survived for the duration of the experiment. One injected male from a food-supplemented nest lost 43.3 g body mass (8.5% of initial body mass) in the 27.6-h DLW measurement interval, had a measured msFMR ($0.821 \text{ mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) that was lower than the resting metabolic rate for this species ($1.197 \text{ mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$; Gabrielsen et al. 1988), and had a water-flux rate of only 34.2 mL/d. These results suggest that either this individual was inactive during the entire measurement interval and consumed neither food nor water, or there were problems with the quality of the blood sample or its analysis. For these reasons this individual was considered an outlier and was not included in subsequent analyses.

Initial body mass at the time of injection varied significantly according to feeding treatment ($F_{[1,60]} = 128.2$, $P < 0.001$) and sex ($F_{[1,60]} = 49.0$, $P < 0.001$). Fed birds were 75–80 g heavier, on average, than control birds and males were heavier than females (Table 2). Body size differed according to sex ($F_{[1,59]} = 89.77$, $P < 0.0001$) but not treatment ($F_{[1,59]} = 0.50$, $P = 0.5$) or treatment by sex ($F_{[1,59]} = 0.43$, $P = 0.5$). Males were typically larger than females in head-bill, tarsus, and flattened-wing lengths (Jodice et al. 2000). Percent total body water for individuals differed according to treatment ($F_{[1,59]} = 102.3$, $P < 0.0001$) but not sex ($F_{[1,59]} = 1.89$, $P = 0.2$) or sex by treatment ($F_{[1,59]} = 0.88$, $P = 0.3$; Table 2). Mean percent total body water for fed birds ($57.7 \pm$

Table 2. Mean body mass, field metabolic rate (FMR), and water-flux rates of chick-rearing Black-legged Kittiwakes in a supplemental-feeding experiment at Middleton Island, Alaska, 27–31 July 1998.

	<i>n</i>	Body mass (g)	FMR (mL CO ₂ ·g ⁻¹ ·h ⁻¹)	DEE (kJ/d)	Percent total body water	Water-influx rate (mL H ₂ O·kg ⁻¹ ·h ⁻¹)	Water-efflux rate (mL H ₂ O·kg ⁻¹ ·h ⁻¹)
Fed females	14	426.8 (7.22)	2.04 (18.8)	571.6 (20.2)	58.4 (4.8)	10.26 (31.4)	10.74 (26.4)
Control females	14	351.1 (8.15)	3.08 (25.8)	695.8 (23.5)	63.6 (2.7)	27.62 (51.0)	27.63 (48.1)
Fed males	16	475.4 (6.07)	2.31 (17.6)	721.3 (18.4)	57.1 (3.8)	11.50 (25.7)	12.04 (21.1)
Control males	18	397.6 (5.51)	2.85 (24.2)	745.1 (23.9)	63.3 (3.2)	22.16 (35.8)	22.37 (33.7)

Note: Numbers in parentheses show the coefficient of variation (%). DEE, daily energy expenditure.

Table 3. Model-selection statistics^a from ANCOVA modeling of mass-specific field metabolic rate (mL CO₂·g⁻¹·h⁻¹) of parent Black-legged Kittiwakes in a supplemental-feeding experiment on Middleton Island, Alaska, 27–31 July 1998.

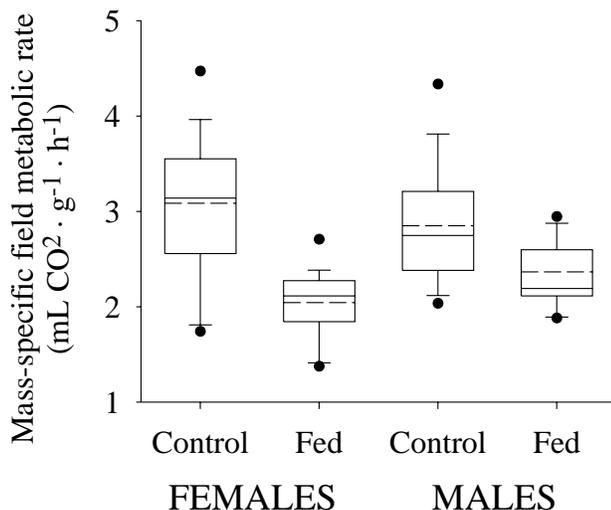
Model parameters ^b	<i>K</i> ^c	ΔAIC _c	AIC _c weight	Cumulative sum of AIC _c weights
Models for females				
Treatment (9)	3	0.00	0.682	0.682
Treatment, body size, body mass (4)	5	2.15	0.263	0.945
Models for males				
Treatment (9)	3	0.00	0.554	0.554
Treatment, body size, body mass (4)	5	1.20	0.304	0.858
Treatment, brood size, chick age (7)	5	4.85	0.049	0.907
All main variables (2)	7	5.13	0.043	0.950

Note: Models are ranked in order from most to least plausible within each sex, given the available data, but only those models from Table 1 that were included in the 95% confidence set of models are presented.

^aTerms specific to the model-selection process are defined in Methods.

^bThe model number is given in parentheses (see Table 1).

^cNumber of estimable parameters + 1 for intercept + 1 for variance estimator.

Fig. 1. Mass-specific field metabolic rates of chick-rearing parent Black-legged Kittiwakes (*Rissa tridactyla*) in a supplemental-feeding experiment on Middleton Island, Alaska, 27–31 July 1998. Boxes display a median line (solid), a mean line (broken), quartiles (box edges), 10th and 90th percentiles (whiskers), and 5th and 95th percentiles (●).

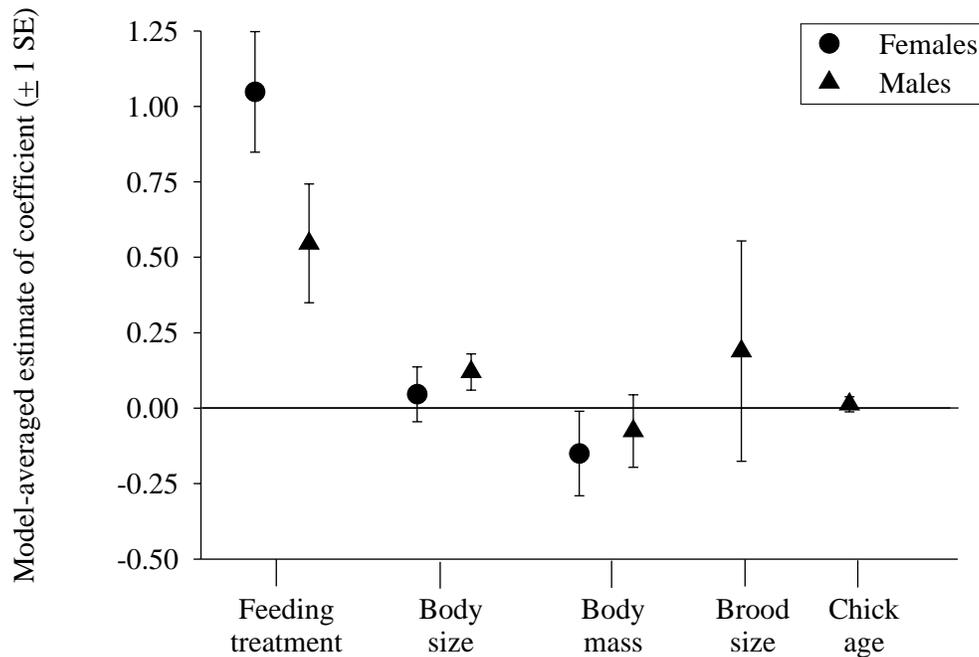
with body mass for either fed or control birds ($r_{\text{fed}} = -0.29$, $r_{\text{control}} = -0.18$).

Field metabolic rates

Feeding treatment had a strong effect on rates of kittiwake energy expenditure (Fig. 1, Table 2). Mass-specific FMRs in fed kittiwakes, which differed slightly between males (2.31 ± 0.40 mL CO₂·g⁻¹·h⁻¹) and females (2.04 ± 0.38 mL CO₂·g⁻¹·h⁻¹; $t_{28} = 1.8$, $P = 0.07$), were substantially lower and less variable than msFMRs of control kittiwakes, which did not differ according to sex (2.95 ± 0.73 mL CO₂·g⁻¹·h⁻¹; $t_{30} = 0.9$, $P = 0.37$). Each step of the model-selection approach confirmed the strong effect of feeding treatment on msFMR within each sex. For example, the model that included only the term for feeding treatment (i.e., model 9 for females and males) best explained the variability in msFMR and was the most parsimonious model tested for each sex (i.e., lowest AIC_c values and highest AIC_c weights; Table 3). Furthermore, female and male “feeding treatment only” models were ca. 2.6 and 1.8 times more likely to be the best model, respectively, than the next best model in the candidate set (Table 3; ratio of AIC_c weights for model 9 to those for model 4 for each sex). Each model that occurred in the 95% confidence set of models for females (models 9 and 4) and males (models 9, 4, 7, and 2) also included the term for feeding treatment, further indicating the importance of this variable in explaining the variability in msFMR. The effect of feeding treatment on msFMR was about twice as strong in females as in males (Fig. 2). The msFMR of fed females

2.5%) was lower than that for controls ($63.4 \pm 1.9\%$), suggesting that fed birds had higher body fat content than controls. Percent total body water was not strongly correlated

Fig. 2. Coefficient and standard error (SE) estimates derived from a model-averaging approach with ANCOVA models of mass-specific FMR ($\text{mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) for parent Black-legged Kittiwakes in a supplemental-feeding experiment on Middleton Island, Alaska, 27–31 July 1998. Only models contained in the 95% confidence set were used for model averaging and only variables contained in those models are presented (see Table 3).



was $1.05 \pm 0.24 \text{ mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ lower than that of control females, while the msFMR of fed males was $0.55 \pm 0.20 \text{ mL CO}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ lower than that of control males. The feeding-treatment model explained 42.7 and 18.8% of the variability in female and male msFMRs, respectively.

Body size and body mass appeared in the 95% confidence set of models for both sexes (Table 3). There was a very slight positive trend towards an increase in msFMR in males of greater body size (Fig. 2). Brood size and chick age appeared in the 95% confidence set of models for males (Table 3), although neither had an effect on male msFMR (Fig. 2).

Daily energy expenditure (i.e., whole-animal FMR) of kittiwakes in this experiment ranged from 403 to 929 kJ/d for fed birds and from 397 to 1149 kJ/d for control birds. Mean daily energy expenditure did not differ significantly between the sexes for control birds ($723.5 \pm 170.9 \text{ kJ/d}$; $t_{30} = 0.8$, $P = 0.4$) but differed significantly between males ($721.3 \pm 132.8 \text{ kJ/d}$) and females ($571.5 \pm 115.7 \text{ kJ/d}$) in the fed group ($t_{28} = 3.3$, $P = 0.003$; Table 2). Energy expenditure rates of our control birds were similar to values reported elsewhere for this species (Gabrielsen et al. 1987; Thompson et al. 1998; Golet et al. 2000; Roby et al. 2000). Energy expenditure rates of fed birds averaged $1.8 \times$ kittiwake BMR, while rates for control birds averaged $2.5 \times$ BMR.

Water turnover

Mass-specific water-influx and -efflux rates ($\text{mL H}_2\text{O}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$) of control birds were about twice those of fed birds for females ($t_{26} > 4.6$, $P < 0.001$) and males ($t_{32} > 5.0$, $P < 0.001$; Table 2). Within individuals, water-efflux rates were nearly identical with water-influx rates for both fed and control birds. There was no significant difference ($P > 0.17$) in mass-specific water-flux rates between males and females

within each treatment group. There was a positive relationship between daily water-influx rate and msFMR for both control males (water-influx rate = $-1.06(\pm 5.97) + 8.10(\pm 2.00) \times \text{msFMR}$; $t_{16} = 4.0$, $P = 0.001$, $R^2 = 0.47$) and control females (water-influx rate = $-5.05(\pm 12.98) + 10.59(\pm 4.08) \times \text{msFMR}$; $t_{12} = 2.59$, $P = 0.02$, $R^2 = 0.31$). There also was a significant positive relationship between daily water-influx rates and msFMR for fed males (water-influx rate = $1.17(\pm 3.56) + 4.49(\pm 1.52) \times \text{msFMR}$; $t_{14} = 2.95$, $P < 0.01$, $R^2 = 0.34$) and fed females (water-influx rate = $0.24(\pm 4.08) + 4.90(\pm 1.96) \times \text{msFMR}$; $t_{12} = 2.49$, $P = 0.03$, $R^2 = 0.29$).

Discussion

Effects of supplemental feeding on FMR

As predicted, msFMRs of kittiwakes raising young were markedly lower when supplemental food was provided at the nest site. Lower energy expenditure in fed kittiwakes likely reflected higher nest-attendance rates relative to control birds (Gill et al. 2002), which likely resulted in a reduction of energetically costly foraging activities by adults (Roby et al. 2000). Supplementally fed kittiwakes also had higher body mass and body fat reserves relative to control birds, despite similarities in structural size. Nestlings of fed birds had higher growth rates compared to nestlings of control birds, and productivity of fed nests was greater than control nests, both in 1998 and in other years (Gill and Hatch 2002; Gill et al. 2002). Therefore, fed kittiwakes increased their reproductive output while simultaneously decreasing parental effort and increasing body condition (i.e., greater body mass and fat reserves). While these results fail to test the competing hypotheses regarding post-hatching loss of body mass in parent seabirds (adaptive vs. reflecting energetic stress; see Gaston and Jones 1989; Croll et al. 1991; Phillips and Furness

1997), they do indicate that parental body mass and fat reserves during chick rearing are sensitive to extrinsic factors such as food availability. Thus, it will be difficult to discriminate between adaptive and stress-related explanations for post-hatching mass loss in parent seabirds without carefully controlled experimental manipulations (Hillstrom 1995; Merila and Wiggins 1997; Cichon 2001).

Parental energy expenditure need not decrease with supplemental feeding. Parents supplemented with food at the nest site can continue to forage at or near their normal rate. This would result in a relatively fixed level of energy expenditure but an increased level of provisioning to nestlings. A fixed level (i.e., no decrease) in parental energy expenditure in response to supplemental feeding has been observed when the amount of supplemental food was insufficient to sustain both parents and nestlings (Moreno et al. 1999), when nestlings derived a fitness benefit from increased provisioning (e.g., when compensating for parasite burdens; Moreno et al. 1999), and when natural food availability was high enough to offset the cost of foraging (Wiehn and Korpimäki 1997; Granadeiro et al. 2000). In contrast, we provided sufficient food for both nestlings and adults, nestling survival rates were high in nests with both fed and control birds, and natural food availability was slightly below average during our study (S.A. Hatch and V.A. Gill, unpublished data).

Gender differences in energy expenditure rates

The difference in msFMR between fed birds and controls was almost twice as much in females as in males. Supplementally fed males also displayed higher FMRs (whole-animal and mass-specific) than supplementally fed females, despite the lack of a gender difference within the control group. These results suggest that the time-activity budgets of fed male kittiwakes differed from those of fed females. We found little support in the literature for sex-specific differences in FMR with respect to food availability. Few studies have directly measured adult energy expenditure as a function of food availability (Bryant and Tatner 1988, 1991; Ellis and Gabrielsen 2001), and those that have often considered just one sex (e.g., Tinbergen and Dietz 1994; Moreno et al. 1999).

Sex-specific differences in FMR in relation to other extrinsic factors such as brood mass, brood age, and brood size have been reported, however (Hails and Bryant 1979; Deerenberg et al. 1995; Moreno et al. 1995). These gender-specific responses have been attributed to differences in the type or duration of parental care exhibited by each sex (Hails and Bryant 1979; Wiehn and Korpimäki 1997). For example, in Eurasian kestrels (*Falco tinnunculus*), which demonstrated gender-specific differences in provisioning rates in response to supplemental food (males displayed a fixed level of effort, females decreased effort; Wiehn and Korpimäki 1997), males hunted more frequently than females and provided food to both the young and their mate. The lower msFMR of fed females than of fed males in our study might be due to reduced activity levels in females compared with males. Nest-attendance data from 1998, however, revealed no difference in attendance rates between fed males and fed females (S.A. Hatch and V.A. Gill, unpublished data), suggesting that any gender difference in activity levels occurred when adults were off the nest. Furthermore,

similar water-flux rates and similar relationships between water-flux rate and FMR for females and males indicated that there were likely no gender differences in food-intake rates in either the control or fed groups which would suggest differences in foraging strategy between the sexes. The higher msFMR of fed males than of fed females may instead reflect a greater tendency for off-duty males to engage in nonforaging activities such as nest defense or prospecting behaviors.

In other gull species where males are larger than females (as is the case in kittiwakes; Jodice et al. 2000), males engage in nest defense and other intraspecific aggressive behaviors more frequently than females, even during the chick-rearing period (Butler and Janes-Butler 1983; Pierotti 1987; Pierotti and Annett 1994). Furthermore, successfully breeding male kittiwakes commonly attend other nest sites even when chicks are present (Cadiou et al. 1994), increasing the potential for aggressive encounters that would require additional expenditure of energy. If male kittiwakes invest more time in nest defense and prospecting behaviors, even during chick rearing, then an increase in food availability and resultant reduction in the time required for foraging (Monaghan et al. 1994; Suryan et al. 2000) would likely have less of an effect on male time-activity budgets, and hence energy expenditure, than on those of females.

Ultimately, however, the direction and magnitude of parental effort in response to supplemental feeding may be related to adult survival costs and the means by which individuals balance current reproductive effort with long-term survival. Daan et al. (1996) described a negative relationship between parental effort and survival rate in Eurasian kestrels. Similarly, Black-legged Kittiwakes nesting in Alaska whose broods were experimentally removed expended energy at a significantly slower rate than controls with broods, and subsequently experienced higher survival rates than control birds (Golet et al. 1998, 2000). We predict that the fed kittiwakes in our study will also experience higher survival rates because supplemental feeding allowed parents to reduce FMR by eliminating the need to forage for themselves and their brood. For example, the metabolic scope of our fed kittiwakes ($1.8 \times \text{BMR}$, on average) was similar to the metabolic scope of kittiwakes in Golet et al.'s (2000) experiment whose broods had been removed ($2.0 \times \text{BMR}$) and who experienced increased survival compared with control birds. This prediction of higher survival rates with lower parental effort appears to be supported for female kittiwakes nesting on the tower on Middleton Island. Resightings of marked adult kittiwakes between 1998 and 1999 indicated that fed females returned at a slightly higher rate than control females, although fed males were resighted at a lower rate than control males (S.A. Hatch and V.A. Gill, unpublished data). Differences in survival rates between the sexes may occur if each sex experiences a different survival curve with respect to FMR or parental effort. Further survival analyses and additional years of data collection may clarify this relationship.

What other factors affected energy expenditure rates?

Model ranking based on AIC_c values and parameter estimates from model averaging clearly showed that none of the other variables we examined had a strong effect on the msFMR of either sex. There was, however, a very slight pos-

itive effect of body size on male msFMR. This sex-specific effect suggests that the relationship between msFMR and body size may be nonlinear when considered across the two sexes. The sex-specific body-size relationships we observed may have resulted from the fact that the time-activity budgets of larger males are different from those of smaller males. Adams et al. (1986) also reported sex-specific differences in the relationship between body size and FMR in Wandering Albatrosses (*Diomedea exulans*), although they did not discuss possible explanations. The lack of brood-size and chick-age effects on msFMR is consistent with the results of most other energetic studies of kittiwakes whose chicks were in the same age range as those in our study (Gabrielsen et al. 1988, 1992; Thompson et al. 1998).

In conclusion, adult kittiwakes raising young reduced their energy expenditure in response to supplemental feeding despite higher productivity than controls. This indicates that both reproductive success and parental effort in kittiwakes can change in response to food availability. Gender differences in the magnitude of response to supplemental feeding suggest that the two sexes may differ in their reproductive roles and behavioral responses to changing environmental conditions during nesting. Lower water turnover per unit of energy expended in fed than in control birds also indicated that fed birds were likely foraging less than control birds. Adjustments in reproductive effort in response to variable foraging conditions may have significant effects on the survival and productivity of individuals, and thus provide substantial fitness benefits for long-lived seabirds such as Black-legged Kittiwakes.

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References

Adams, N.J., Brown, C.R., and Nagy, K.A. 1986. Energy expenditure of free-ranging wandering albatrosses (*Diomedea exulans*). *Physiol. Zool.* **59**: 583–591.

- Adams, N.J., Abrams, R.W., Siegfried, W.R., Nagy, K.A., and Kaplan, I.R. 1991. Energy expenditure and food consumption by breeding Cape gannets. *Mar. Ecol. Prog. Ser.* **70**: 1–9.
- Bautista, L.M., Tinbergen, J.M., Wiersma, P., and Kacelnik, A. 1998. Optimal foraging and beyond: how starlings cope with changes in food availability. *Am. Nat.* **152**: 543–561.
- Bryant, D.M. 1991. Constraints on energy expenditure by birds. *Proc. Int. Ornithol. Congr.* **20**: 1989–2001.
- Bryant, D.M. 1997. Energy expenditure in wild birds. *Proc. Nutr. Soc.* **56**: 1025–1039.
- Bryant, D.M., and Tatner, P. 1988. The costs of brood provisioning: effects of brood size and food supply. *Proc. Int. Ornithol. Congr.* **19**: 364–379.
- Bryant, D.M., and Tatner, P. 1991. Intraspecific variation in avian energy expenditure: correlates and constraints. *Ibis*, **133**: 236–245.
- Bryant, D.M., and Westerterp, K.R. 1983. Short-term variability in energy turnover by breeding house martins: a study using doubly-labelled water. *J. Anim. Ecol.* **52**: 525–543.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Butler, R.G., and Janes-Butler, S. 1983. Sexual differences in the behavior of adult Great Black-backed Gulls (*Larus marinus*) during the pre- and post-hatch periods. *Auk*, **100**: 63–75.
- Cadiou, B., Monnat, J.Y., and Danchin, E. 1994. Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural patterns and the role of squatting in recruitment. *Anim. Behav.* **47**: 847–856.
- Cichon, M. 2001. Body-mass changes in female Collared Flycatchers: state-dependent strategy. *Auk*, **118**: 550–552.
- Croll, D.A., Gaston, A.J., and Noble, D.G. 1991. Adaptive loss of mass in Thick-billed Murres. *Condor*, **93**: 496–502.
- Daan, S., Deerenberg, C., and Dijkstra, C. 1996. Increased daily work precipitates natural death in the kestrel. *J. Anim. Ecol.* **65**: 539–544.
- Davis, J.N., Todd, P.M., and Bullock, S. 1999. Environment quality predicts parental provisioning decisions. *Proc. R. Soc. Lond. B Biol. Sci.* **266**: 1791–1797.
- Deerenberg, C., Pen, I., Dijkstra, C., Arkies, B.-J., Visser, G.H., and Daan, S. 1995. Parental energy expenditure in relation to manipulated brood size in the European kestrel (*Falco tinnunculus*). *Zoology (Jena)*, **99**: 39–48.
- Ellis, H.I., and Gabrielsen, G.W. 2001. Energetics of free-ranging seabirds. In *Biology of marine birds*. Edited by E.A. Schreiber and J. Burger. CRC Press, Boca Raton, Fla. pp. 359–408.
- Gabrielsen, G.W., Mehlum, F., and Nagy, K.A. 1987. Daily energy expenditure and energy utilization of free-ranging Black-legged Kittiwakes. *Condor*, **89**: 126–132.
- Gabrielsen, G.W., Mehlum, F., and Karlsen, H.E. 1988. Thermoregulation in four species of arctic seabirds. *J. Comp. Physiol. B*, **157**: 703–708.
- Gabrielsen, G.W., Klaassen, M., and Mehlum, F. 1992. Energetics of Black-legged Kittiwake *Rissa tridactyla* chicks. *Ardea*, **80**: 29–40.
- Gaston, A.J., and Jones, I.L. 1989. The relative importance of stress and programmed anorexia in determining mass loss by incubating Ancient Murrelets. *Auk*, **106**: 653–658.
- Gessaman, J.A., and Nagy, K.A. 1988. Energy metabolism: errors in gas-exchange conversion factors. *Physiol. Zool.* **61**: 507–513.
- Gill, V.A., and Hatch, S.A. 2002. Components of productivity in Black-legged Kittiwakes (*Rissa tridactyla*): response to supplemental feeding. *J. Avian Biol.* **33**: 113–126.
- Gill, V.A., Hatch, S.A., and Lanctot, R.B. 2002. Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes (*Rissa tridactyla*). *Ibis*. In press.

- Golet, G., Irons, D.B., and Estes, J.A. 1998. Survival costs of chick rearing in Black-legged Kittiwakes. *J. Anim. Ecol.* **67**: 827–841.
- Golet, G., Irons, D.B., and Costa, D. 2000. Energy costs of chick rearing in Black-legged Kittiwakes. *Can. J. Zool.* **78**: 982–991.
- Granadeiro, J.P., Bolton, M., Silva, M.C., Nunes, M., and Furness, R.W. 2000. Responses of breeding Cory's shearwater (*Calonectris diomedea*) to experimental manipulation of chick condition. *Behav. Ecol.* **11**: 274–281.
- Hails, C.J., and Bryant, D.M. 1979. Reproductive energetics of a free-living bird. *J. Anim. Ecol.* **48**: 471–482.
- Hillstrom, L. 1995. Body mass reduction during reproduction in the Pied Flycatcher (*Ficedula hypoleuca*): physiological stress or adaptation for lowered costs of locomotion? *Funct. Ecol.* **9**: 807–817.
- Jacobsen, K.-O., Erikstad, K., and Sæther, B.-E. 1995. An experimental study of the costs of reproduction in the kittiwake (*Rissa tridactyla*). *Ecology*, **76**: 1636–1642.
- Jodice, P.G.R., Lanctot, R.B., Gill, V.A., Roby, D.D., and Hatch, S.A. 2000. Sexing adult Black-legged Kittiwakes by DNA, behavior, and morphology. *Waterbirds*, **23**: 407–417.
- Lalonde, R.G. 1991. Optimal offspring provisioning when resources are not predictable. *Am. Nat.* **138**: 680–686.
- Lifson, N., and McClintock, R. 1966. Theory of the use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* **12**: 46–74.
- Merila, J., and Wiggins, D.A. 1997. Mass loss in breeding Blue Tits: The role of energetic stress. *J. Anim. Ecol.* **66**: 452–460.
- Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., Walton, P., and Burns, M.D. 1994. The influences of changes in food abundance on diving and surface-feeding seabirds. *Can. Wildl. Serv. Occ. Pap. No. 91*. pp. 10–19.
- Moreno, J., Cowie, R.J., Sanz, J.J., and Williams, R.S.R. 1995. Differential response by males and females to brood manipulations in the pied flycatcher (*Ficedula hypoleuca*): energy expenditure and nestling diet. *J. Anim. Ecol.* **64**: 721–732.
- Moreno, J., Merino, S., Potti, J., Leon, A.D., and Rodriguez, R. 1999. Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. *Behav. Ecol. Sociobiol.* **46**: 244–251.
- Nagy, K.A., and Costa, D. 1980. Water flux in animals: analyses of potential errors in the tritiated water method. *Am. J. Physiol.* **238**: R454–R465.
- Neter, J., Wasserman, W., and Kutner, M.H. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. Irwin, Boston.
- Norberg, R.A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching methods. *J. Anim. Ecol.* **46**: 511–529.
- Nudds, R.L., and Bryant, D.M. 2000. The energetic costs of short flight in birds. *J. Exp. Biol.* **203**: 1561–1572.
- Phillips, R.A., and Furness, R.W. 1997. Sex-specific variation in the loss of mass by breeding Arctic Skuas. *J. Avian Biol.* **26**: 313–320.
- Pierotti, R. 1987. Behavioral consequences of habitat selection in the herring gull. *Stud. Avian Biol.* **10**: 119–128.
- Pierotti, R., and Annett, C. 1994. Patterns of aggression in gulls: asymmetries and tactics in different social categories. *Condor*, **96**: 590–599.
- Potti, J., Moreno, J., and Merino, S. 1999. Repeatability of parental effort in male and female Pied Flycatchers as measured with doubly labeled water. *Can. J. Zool.* **77**: 174–179.
- Roby, D.D., Jodice, P.G.R., and Turco, K.R. 2000. Diet composition, reproductive energetics, and productivity of seabirds damaged by the Exxon Valdez oil spill. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 00163G). U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis.
- Schmid-Hempel, P., and Wolf, T. 1988. Foraging effort and life span of workers in a social insect. *J. Anim. Ecol.* **57**: 509–522.
- Speakman, J.R. 1997. Doubly labelled water: theory and practice. Chapman and Hall, New York.
- Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.
- Suryan, R.M., Irons, D.B., and Benson, J. 2000. Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect on reproductive success. *Condor*, **102**: 374–384.
- Thompson, D.L., Furness, R.W., and Monaghan, P. 1998. Field metabolic rates of kittiwakes (*Rissa tridactyla*) during incubation and chick rearing. *Ardea*, **86**: 169–175.
- Tinbergen, J.M., and Dietz, M.W. 1994. Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* **8**: 563–572.
- Trivers, R.L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. Edited by B. Campbell. Aldine, Chicago. pp. 136–197.
- Visser, G.H. 2001. Chick growth and development in seabirds. *In* Biology of marine birds. Edited by E.A. Schreiber and J. Burger. CRC Press, Boca Raton, Fla. pp. 439–465.
- Visser, G.H., Boon, P.E., and Meijer, H.A.J. 2000a. Validation of the doubly labeled water method in Japanese Quail *Coturnix c. japonica* chicks: is there an effect of growth rate? *J. Comp. Physiol. B*, **170**: 365–371.
- Visser, G.H., Dekinga, A., Achterkamp, B., and Piersma, T. 2000b. Ingested water equilibrates isotopically with the body water pool of a shorebird with unrivaled water fluxes. *Am. J. Physiol.* **279**: R1795–R1804.
- Wiehn, J., and Korpimäki, E. 1997. Food limitation on brood size: experimental evidence in the Eurasian kestrel. *Ecology*, **78**: 2043–2050.
- Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.